SOCIAL ENCOUNTERS BETWEEN MALE BROWN SPIDERS, LOXOSCELES GAUCHO (ARANEAE, SICARIIDAE)

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ABSTRACT. Twenty-two interactions between males of *Loxosceles gaucho* Gertsch 1967 were investigated in order to study its intrasexual interactions and level of aggressiveness. Aggression by lunges or bites was observed in just 22.7% of the trials and three behaviors were identified as aggression-attenuating mechanisms: a hug; fleeing, and a postural pattern (POS). Interactions took place in 59.1% of the trials and the pairs interacted using one or two behavioral patterns (vibratory and/or postural). The vibratory pattern (VIB) consisted of foreleg vibration, palpal drumming, and abdominal pulsation and was used by both resident and intruder opponents. The postural pattern (POS) was used exclusively by resident males and it was similar to the behavioral pattern of sexually receptive *L. gaucho* females; in these cases the intruder male responded using the VIB. In conclusion, the interaction between adult *L. gaucho* males is usually non-aggressive. The behaviors described in this study possibly promote group-living and help to explain the gregarious populations of recluse spiders. Intra-specific sexual mimicry can occur in these interactions, but this hypothesis requires further investigation.

Keywords: Aggression, gregariousness, male-male interaction, sexual mimicry

Aggression takes place when an animal attacks or threatens an opponent. Findings in Game Theory have shown that aggressive or agonistic encounters between conspecifics usually minimize and/or delay aggression, improving the individual fitness of the opponents (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Whitehouse 1997). In malemale spider interactions, some particular characteristics or behaviors can act as aggressionattenuating mechanisms, such as differences in weight (Suter & Keyley 1984) or size (Whitehouse 1997; Bridge et al. 2000; Taylor & Jackson 2003), and ritualized behaviors (Lubin 1986). Even the presence/absence of determined elements in the contest area can affect opponent aggressiveness, as shown by Wells (1988) for male Trite parvula (Bryant 1935) (Araneae, Salticidae), which escalate contests in the presence of a female model.

In addition, aggressiveness and tolerance are key factors to understand the evolution of social behavior in spiders (see Uetz & Hieber 1997). Most spiders are essentially solitary, but a few species have different degrees of sociability that range from aggregations of individual webs to cooperative brood care (Avilés 1997). There are species that exhibit social plasticity, i.e., that do not display obligatory social behavior. These species are a primary animal model for the study of aggressionattenuating mechanisms. This is the case of the recluse spiders that are generally solitary but can aggregate around and inside buildings (Bücherl 1961; Horner & Stewart 1967; Fischer & Vasconcellos-Neto 2005; Marques-da-Silva et al. 2006).

Individuals of the recluse spider Loxosceles gaucho Gertsch 1967 (Araneae, Sicariidae) are usually solitary in their natural habitat, as in the Butantan Institute woods (Japyassú et al. 2003). However, like other recluse spiders they aggregate in manmade environments or in disturbed natural habitats. For instance Stropa & Pinhal (2005) found adult L. gaucho aggregating in brick piles deposited on the ground; and Stropa (2004) reported that two males of this species may share a small retreat in the field during the day. At night, however, males commonly wander searching for females. The silk produced by both males and females is easily recognized in the field and is abundant, at least in the Botanic Garden from Botucatu, Brazil. The silk covers portions of the spiders' retreats which are mainly in crevices and the cavities of the litter. The web of L. gaucho is thin, white, and irregular and covers the substrate like a thin sheet. L. gaucho also occurs in house yards but there is no evidence that it prefers this habitat (Stropa & Pinhal 2005). It is

endemic from southwestern Brazil and it occurs mainly in the states of São Paulo and Paraná (Marques-da-Silva & Fischer 2005).

In this study, a resident-intruder paradigm was used to examine interactions between male *L. gaucho* in order to study its intrasexual aggressiveness and to explore the possible influences of the male-male interactions on the lifestyle of recluse spiders. Voucher specimens are deposited at the Coleção de Aranhas do Departamento de Zoologia, UNESP, Campus de Botucatu, UBTU.

METHODS

Test animals and holding conditions.—Fortyfour adult male *L. gaucho* were hand-collected from stalk crevices of *Eucalyptus* sp. at the Botanic Garden from IB, UNESP, Botucatu, Brazil (22°59'S, 48°26'W). These animals were maintained in individual glass test tubes (85 mm \times 25 mm internal diameter) for about 30 days before the experiments, and fed once a week on insects collected by sweeping. About 3 days before the experiment, the spiders were fed in excess (5 *Musca domestica* per spider) to balance satiation level. The forty-four spiders were used for twenty-two pairwise encounters.

The encounters.-Twenty-two encounters between males were carried out using an intruderresident paradigm. One spider, designated as the resident, was placed inside the arena (a transparent plastic cage, 110 mm diameter \times 70 mm high). This area was about 30-50% bigger than the retreats of L. gaucho in the field. One week after this, time enough for the resident to spin its irregular web, the external transparent tube (60 mm long \times 40 mm diameter) attached to the arena was disconnected. Another spider, designated as the intruder, was introduced in the tube that was reconnected to the arena. At this point, both the resident and the intruder were allowed to encounter each other.

Spider pairs were selected in order to balance the relative weight between the opponents. Thus, in 11 encounters weight difference was higher than 10% while in the other 11 encounters weight difference was lower than 10%. In the trials with either high or low relative weight, the frequency of residents and intruders with higher weight was also balanced, i.e., residents were heavier in five trials and intruders were heavier in the other six trials. Spiders were weighed with a Mettler H20T balance (160 g; 0.01 mg) one day before experiments. The avg. weight of the specimens was 55.23 ± 15.42 mg (mean \pm SD). Each spider was tested only once.

One week before the encounter, one spider of each pair was marked with a nail polish dot on the abdomen to facilitate individual recognition. No toxic effects of this product were observed. Temperature and relative air humidity were kept at approximately 25° C and 70% inside the arenas.

The encounters were tape recorded (VHS system) from above the arenas. Each encounter ended when a "losing" spider was identified (e.g., when either one of the opponents ran away from the rival or abandoned the interaction by moving backwards).

Data analyses.—The behavioral sequences were qualitatively and quantitatively described in a flow diagram (Fig. 1) so that behavioral pathways that ended in aggression and nonaggression could be identified. Aggressive behaviors included lunges or bites (Table 1). Encounters without occurrence of these lunges or bites were defined as non-aggressive encounters. The predominance of these aggressive and non-aggressive encounters was tested using the Chi-square goodness-of-fit test with Yates correction.

RESULTS

The general pattern of encounters between male L. gaucho began with the intruders walking into the arena and touching the residents' web (n = 21). In one instance, the resident moved first. After these first movements, in all cases, (n = 22), the intruders vibrated their body appendices; a pattern designated as "VIB" (Table 1 and Fig. 1). Following this, the residents responded by fleeing (n = 9) or interacted using the VIB pattern, i.e., similar to the intruders' behavior (n = 8). The other residents interacted using a postural performance rather than movements, a pattern designated as "POS" (n = 5) (Table 1 and Fig. 1). The duration of the VIB-VIB encounters was of 3-8 min while the duration of the VIB-POS encounters was much longer, 18-37 min. In both types of encounters, the spiders of each pair approached and touched each other with their forelegs (Fig. 1). With the VIB-VIB interaction, when the opponents reached the face-to-face position, they overlapped their forelegs (behavior named "hug" - Table 1) and

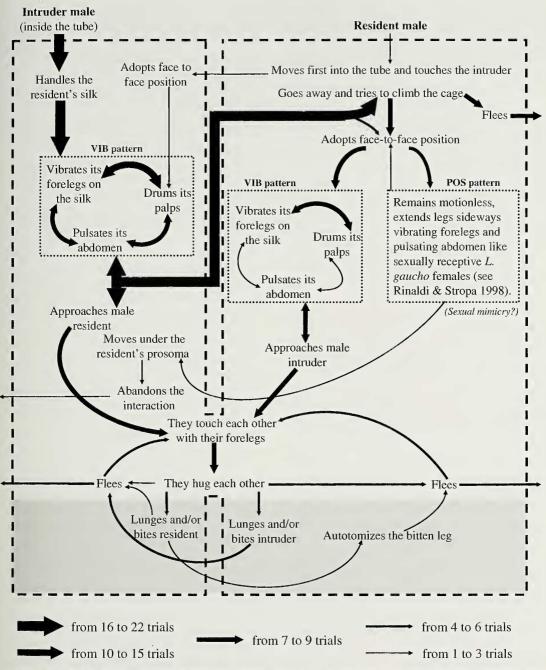


Figure 1.—Flow diagram of the male-male interaction of *L. gaucho* (n = 22). Dashed lines delimit the context. Dotted lines indicate the determined behavioral patterns (movements and/or postures of specific portions of the spider's body). The gray line delimits the period of aggression (area below it). Thickness of arrows indicates the frequency with which the behaviors were observed.

one spider of the pair either fled or lunged at its opponent. On the other hand, when VIB-POS interaction took place, the intruder advanced under the resident's prosoma and then either abandoned the interaction (n = 3), or fled (n = 2). In these last two cases the interaction was longer than 30 min and the residents became aggressive, i.e., they changed from POS into

Patterns	Behaviors	Description
VIB	Foreleg vibration	Simultaneous vertical movement of the pairs of legs whose tarsi touch the resident's silk.
	Palpal drumming	Alternate vertical palp movements
	Abdominal pulsation 1	Vertical and horizontal abdomen movements
POS	Abdominal pulsation 2 Motionless Legs sideways	Just vertical movements and slower than the abdominal pulsation I Stop walking Extension of all legs sideways
	Hug	Opponents overlap their forelegs (opponents' forelegs touch and bear each other)
	Lunge	One spider jumps abruptly towards its opponent
	Bite	Chelicerae hold a part of the body of a spider and the fangs pierce the cuticle

Table 1.—Behavioral patterns and conspicuous behaviors of the male-male interaction of L. gaucho.

VIB pattern and immediately the opponents hugged each other and the residents lunged against the intruders.

Non-aggressive encounters were preponderant (77.3%) (n = 17: $\chi^2_c = 5.500$, P < 0.025). Aggression (occurrence of lunges or bites) took place in just five encounters (22.7%) (Fig. 1), always after the VIB-VIB interaction, even when the residents started their interaction using the POS pattern. In a single aggressive encounter there was physical injury; the injured spider autotomized the bitten leg (Fig. 1).

DISCUSSION

The present study indicates that interactions between male L. gaucho are predominantly non-aggressive, at least in the resident-intruder paradigm. When aggression (lunges or bites) took place, it occurred only after the hug. But in this species, the hug does not necessarily trigger aggression since it also occurred in nonaggressive male-male (Fig. 1) and female-female encounters (Stropa & Rinaldi 2001). The hug is possibly used by adult L. gaucho spiders to evaluate fighting ability and/or the size of their opponents, allowing for a decision between fleeing or fighting. If this is true; the hug is an aggression-attenuating mechanism since it delays aggression and, as a consequence, improves individual fitness. This situation is predicted in asymmetric animal contests (Maynard Smith & Price 1973; Maynard Smith & Parker 1976; Whitehouse 1997).

Two more conspicuous aggression-attenuating mechanisms were found: the fleeing and the POS pattern. Residents fled in 9 of the 22 trials without further interaction with the intruders. This is expected because male spiders may not establish residence in the natural habitat since they move while searching for females (Foelix 1982). Moreover, they are not likely to defend empty territories (e.g., without females or other resources). The present study indicates that intruder males were always interested in interacting with residents displaying the VIB pattern (Fig. 1). However, this interaction was also expected since information about habitat quality can be obtained from other spiders or simply from silk (Hodge & Storfer-Isser 1997; Schuck-Paim & Alonso 2001; Bilde et al. 2002).

An unexpected aggression-attenuating mechanism observed in this study is the POS pattern displayed by five of the 22 residents. In these trials the resident was nearly motionless with the legs stretched sideways, pulsating its abdomen slower than the intruders, and had its prosoma lifted by the intruder advancement. According to Rinaldi & Stropa (1998), when female L. gaucho are sexually receptive, they allow males to lift their prosoma to copulate. Males use their own prosoma to lift females, such as the intruders did in the present study. This may not be a simple case of mistaken sexual identity because there were differences in the male-male interaction observed here and the male-female interaction reported by Rinaldi and Stropa (1998). Males interact with females only by palpal drumming, foreleg vibration and abdomen pulsation (Rinaldi & Stropa 1998); e.g., the VIB pattern seen here. Female L. gaucho become receptive for mating only by stretching their legs sideways, pulsating their abdomen slowly and keeping themselves nearly motionless (Rinaldi & Stropa 1998); i.e., these

females use only the POS pattern in the sexual interaction. In the present study, male *L. gaucho* used both the VIB and POS patterns in the male-male interaction.

It is possible that the male intruders were courting and trying to copulate with the male residents as if they were receptive females. For spiders, this may be an instance of intraspecific sexual mimicry, which is when an animal gets some advantage over its conspecific opponent by present itself as if it is an individual of the opposite sex. Further investigation is needed to corroborate this hypothesis since only five cases are described in the present study. Sexual mimicry in spiders has been reported only in interspecific interactions such as the bolas spider Mastophora sp. attracting prey (Eberhard 1977; Stowe et al. 1987; Yeargan 1994) and Portia fimbriata Doleschall 1859 mimicking a male of Euryattus sp. (Salticidae) to attack the female hiding in a leaf (Jackson & Wilcox 1990).

The two encounters in which resident males used POS followed by VIB are intriguing and possibly indicate that male *L. gaucho* has some behavioral plasticity. In both cases, the contest escalated to aggressive behaviors after the resident displayed VIB, and the resident won the contest. According to Horel et al. (1996), behavioral plasticity is a pre-adaptation for social life in spiders since it amplifies the intraspecific tolerance. This hypothesis may explain male pairs of this species sharing retreats in the field during the day (Stropa 2004).

In conclusion, the intraspecific interaction of male L. gaucho in the resident-intruder paradigm is usually non-aggressive. This profile is a result of the three aggression-attenuating mechanisms identified: the hug, the fleeing and the POS pattern. These mechanisms may facilitate group living. Recluse spiders have been classified as solitary and territorial (Bücherl 1961; Weens & Whitcomb 1975; Japyassú et al. 2003), but according to several reports they also live in conspecific aggregations and infest manmade environments (Bücherl 1961; Levi & Spielman 1964; Howner & Stewart 1967; Waldron et al. 1975; Fischer & Vasconcellos-Neto 2005; Marques-da-Silva et al. 2006). The investigation of the causes of these aggregations might reveal the main factors modulating the lifestyle of recluse spiders and might elucidate mechanisms that minimize

infestation in manmade environments where *Loxosceles* can become a public health problem. However, interaction is only one factor to be considered and it is certainly linked to other variables such as resource availability and habitat architecture.

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